Variation in Molt Increment Patterns and Life-history Sequences in a Lobster, *Homarus americanus*, Population

G.P. Ennis

Science, Oceans and Environment Branch
Aquatic Resources Division
Fisheries and Oceans Canada
80 East White Hills Road
P.O. Box 5667
St. John's, NL A1C 5X1

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G.P. Ennis

Science, Oceans and Environment Branch
Department of Fisheries and Oceans
P.O. Box 5667
St. John's, NL A1C 5X1

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ABSTRACT

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A tag-recapture study that yielded multi-consecutive-year life-history sequences for individual lobsters was conducted in a Newfoundland area closed to commercial fishing from 1976-89. Carapace length (CL) molt increments for individual lobsters varied but there was no consistent pattern in the chronological sequence of molts. Intermolt periods of up to 5 years were recorded – there was no indication that molt increment was affected by the number of years between molts. In the case of females, the previous year's life-history event (i.e. molt, spawn, both or neither) had no effect on molt increment. Patterns of molt increment variation in relation to size were different for early (1976-78) and later (1984-86) years of the study period.

For the most part, females alternated between molting and spawning in consecutive summers. In 1976-78, 79% of the females for which two-consecutive-year life-history sequences were recorded molted and spawned in alternate summers; this was up to 90% for the 1984-86 period. This pattern was maintained in 88% and 54% of the females for which three- and four-consecutive-year sequences, respectively, were recorded during the study. Other than molting and spawning in alternate summers, life-history sequences included molting or spawning in each of two consecutive summers as well as molting and spawning or doing neither in a particular summer.

Life-history data collected before and after significant changes in a lobster population can yield different estimates of parameters that are important components of fishery assessment models.

RÉSUMÉ

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De 1976 à 1989, une étude de marquage-recapture a été menée dans une zone de Terre-Neuve où la pêche commerciale était interdite pour suivre la séquence de mues et de fraies d'homards individuels sur plusieurs années consécutives. L'accroissement en longueur de la carapace de chaque homard a varié d'une mue à l'autre sans suivre un ordre chronologique particulier. Selon nos observations, il peut s'écouler jusqu'à 5 ans entre deux mues, et il ne semble pas y avoir de relation entre l'allongement de la carapace au moment d'une mue et le nombre d'années écoulées depuis la dernière. Le fait qu'une femelle ait mué et/ou frayé ou non l'année précédente n'a eu aucun effet sur l'allongement de sa carapace à la mue. La relation entre la variation de l'allongement et la taille différait entre le début (1976-78) et la fin de la période d'étude (1984-86).

D'une année à l'autre, la plupart des femelles ont alterné entre la mue et la fraie, ce fut le cas pour 79 et 90 % des femelles capturées deux années de suite entre, respectivement, 1976 et 1978, et 1984 et 1986. Cette alternance a été observée chez 88 et 54 % des femelles capturées respectivement trois et quatre années de suite. Autrement, les homards pouvaient frayer ou muer deux années de suite, ou avoir une fraie et une mue ou aucune des deux le même été.

Les données de ce type recueillies avant et après d'importants changements dans la population de homards peuvent donner des estimations différentes de paramètres importants dans les modèles d'évaluation de la pêche.

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INTRODUCTION

Major life-history events such as molting, mating, spawning and hatching occur repeatedly throughout the life span of individual American lobsters, *Homarus americanus*, with varying periodicity (Waddy *et al.* 1995). In Newfoundland lobster populations, these events occur for the most part during July and August each year. At sizes >60 mm CL, individual lobsters molt no more than once during the summer season (Ennis 1978). Some females that are spawning for the first time molt and spawn in the same summer (Ennis 1984; Waddy *et al.* 1995). Usually, however, maturing females molt and mate in one summer, spawn the next, hatch the eggs about one year later, then molt and mate again shortly afterwards. This 2-year cycle is the norm following initial maturation. Data pertaining to molting and spawning in particular are critically important inputs to assessment models for fisheries management purposes. Biological parameters for use in such models are usually estimated from single observations on individual lobsters from a short time period. There is usually no indication from such observations of the extent of variation within individuals with respect to successive events or for the population as a whole between different periods.

A tag-recapture study that yielded multi-consecutive-year life-history sequences for individual lobsters was conducted in a Newfoundland area while it was closed to commercial fishing from 1976 to 1989. Included were observations on consecutive molt increments, intermolt periods and molt/spawn sequences. The purpose here is to examine molt increment variability and variability in life-history sequences within individuals. Patterns of molt increment variability in relation to size for different population components at different times during the study period are also considered.

MATERIAL AND METHODS

The lobster grounds adjacent to Shag Rocks in Long Harbour, Placentia Bay on the southeast coast of Newfoundland (Fig. 1) were closed to commercial fishing in 1976. The closure was maintained annually up to and including 1989. Each year short periods (2-3 weeks) of research fishing using regular commercial traps were conducted in May or June coinciding with the annual spring fishing season in the surrounding area and usually again in autumn following summertime life-history activity. The CL of each lobster was measured to the nearest 1.0 mm and sex, presence of eggs and shell condition were also recorded. Within a few minutes of being removed from a trap each lobster was tagged with a sphyrion tag and released close to where the trap was hauled. Fishermen recaptured some of the tagged lobsters on nearby fishing grounds around Long Harbour (Fig. 1) but the vast majority was recaptured around the Shag Rocks during periods of research fishing. Those recaptured at the Shag Rocks were carefully reexamined; observations were recorded as at initial capture, and released again. Tags were removed from those recaptured by fishermen after examination.

Molt increments in relation to premolt CL and premolt-postmolt CL relationships were determined separately for data collected in 1976-78 (early years) and 1984-86 (later years) and compared.

RESULTS

POPULATION CHANGES

Following closure of the Shag Rocks to commercial lobster fishing in 1976, composition of the population shifted to larger sizes, although there continued to be a large overlap in range of sizes, and a higher proportion of ovigerous females (Fig. 2). Among the males in 1976 (CL range 68-120 mm), only 6.4% compared to 37.8% in 1984 (CL range 77-147 mm) were larger than 110 mm. Similarly, among the females in 1976 (CL range 66-119 mm), 1.8% compared to 31.1% in 1984 (CL range 75-137 mm) were larger than 110 mm. Among females the percentage ovigerous increased from 8.2% to 31.6% (chi-square test; $P < 0.001$) among 80-95 mm animals and from 8.1% to 29.3% ($P < 0.001$) among 96-110 mm animals.

MOLT INCREMENT IN RELATION TO PREMOLT SIZE

There was considerable variability in single molt CL increments for both sexes. For males 69–128 mm CL, molt increments ranged from 5 to 24 mm and for females from 70 to 133 mm CL, they ranged from 5 to 22 mm (Tables 1 and 2).

Premolt CL-molt increment regressions indicated no slope ($P = 0.117$) in 1976-78 but a positive slope ($P = 0.0001$) in 1984-86 for males (Fig. 3). The slope was negative ($P = 0.001$) for females that were nonovigerous prior to molting in 1976-78 but there was no slope for ovigerous females in 1976-78 ($P = 0.19$) or in 1984-86 ($P = 0.94$) (Fig. 4). There were too few observations on known nonovigerous specimens in 1984-86 for similar analysis.

VARIATION IN CONSECUTIVE MOLT INCREMENTS

There was substantial variability in CL increments between consecutive molts for individual lobsters. For those that a second molt increment was recorded (55 males and 74 females), the difference ranged from 7 mm less to 8 mm greater than the first for males and for females from 9 mm less to 7 mm greater than the first (Table 4). Overall, the second increment was greater than the first in 64% of the males and 42% of the females and less than the first in 25% of the males and 39% of the females. The data indicate a lower incidence of larger second molt increments among the smaller (70-80 mm) females and larger (>100 mm) animals of both sexes.

Among the females whose first molt increment was more than 1 s.d. larger than the mean, the second increment was smaller than the first, and those whose first increment was more than 1 s.d. smaller than the mean, the second was larger than the first (Table 5). This pattern held for half the males in each category. The difference between largest and smallest among three consecutive molt increments for individuals ranged from 2 to 7 mm for four males and from 1 to 4 mm for seven females.

MOLT INCREMENT IN RELATION TO DIFFERENT LIFE-HISTORY SEQUENCES

Single molt increments following intermolt periods from 1 to 5 years for males and 1, 2 and 4 years for females were obtained. There were too few observations for detailed analysis by size group. However, there was considerable variation in molt increment for 1- to 3-year intermolts at all sizes for which there were multiple observations and the few observations for 4- and 5-year intermolts included molt increments that varied within similar ranges (Fig. 5, Table 6). The data for 91-110 CL males suggest a decline in mean molt increment with longer intermolt periods, however, comparisons of the small samples indicated no significant differences ($P > 0.11$) between 1-, 2- and 3-year intermolts. Two-year intermolts dominated the observations for females. While the mean molt increment for the small number of 1-year intermolts for 81-110 CL females was slightly larger, comparison with the data for 2-year intermolts indicated the difference was not significant ($P = 0.62$). Molt increments recorded for two females after 4-year intermolts were well below their 1984-86 CL molt increment regression line as was one for a male after a 5-year intermolt. One for a male after a 4-year intermolt, however, was well above the line.

For females there was also considerable variability in molt increments following various life-history events. For larger females, most of which had spawned the previous year, there was much less variation than for 75-95 mm CL animals (Fig. 6). Molt increments were also less variable for those that had also molted the previous year (range 6–11 mm, mean = 8.2 mm, N = 5) but there were too few observations for comparisons. For 75 – 95 mm CL females that had neither molted nor spawned the previous year, the mean increment (mean = 11.7 mm CL, N = 9) was greater than for those that had spawned the previous year (mean = 9.2 mm CL, N = 54) (Mann-Whitney test; $P = 0.02$). For those that molted and spawned in the same year, the mean increment (mean = 10.3 mm CL, N = 18) was not significantly different ($P \geq 0.50$) from either of the latter two.

PREMOLT–POSTMOLT CL RELATIONSHIPS

Premolt–postmolt CL regressions were compared by analysis of covariance. For males, slopes for the 1976-78 and 1984-86 regressions were significantly different ($P = 0004$). The slope for the 1976-78 regression (0.953) was not significantly different from 1 ($P = 0.12$) and that for the 1984-86 regression (1.096) was significantly greater than 1 ($P = 0.0001$) (Fig. 7).

Slopes for the regressions for ovigerous and nonovigerous females in 1976-78 bordered on being significantly different ($P = 0.05$). The slope for the ovigerous females (0.955) was not significantly different from 1 ($P = 0.19$) but, for nonovigerous, it (0.839) was significantly less than 1 ($P = 0.0008$) (Fig.8). In 1984-86 there were too few observations on females that were know to be nonovigerous prior to molting for a comparison with 1976-78. For ovigerous females the slopes of the regressions for 1976-78 (0.955) and 1984-86 (1.002) were not significantly different ($P = 0.26$) and neither differed significantly from 1 ($P = 0.19$ and 0.94. respectively) (Fig. 9).

For each of the two periods, data for all females were combined. In 1976-78 N = 198 which included 114 that were nonovigerous prior to molting and 84 that were ovigerous. In 1984-86, N = 88 which included 5 nonovigerous, 54 ovigerous and 29 whose status prior to molting was unknown. The slopes of these two regressions were significantly different (P = 0.0002) (Fig. 10). For the 1976-78 regression the slope (0.860) was significantly less than 1 (P = 0.0001) and for the 1984-86 regression it (0.990) was not significantly different from 1 (P = 0.52).

CONSECUTIVE-YEAR LIFE-HISTORY SEQUENCES IN FEMALES

For the most part, females alternated between molting and spawning in consecutive summers. In 1976-78, 79% of the females for which two-consecutive-year life-history sequences were recorded molted and spawned in alternate summers; this was up to 90% for the 1984-86 period (Table 7). Other than molting and spawning in alternate summers, life-history sequences included molting or spawning in each of two consecutive summers, molting and spawning in the same summer followed by molting or spawning the next, and neither molting nor spawning in a particular summer following one or the other the previous summer (Table 7).

Molting and spawning in alternate summers was the pattern maintained in 89% (N = 72) and 54% (N = 13) of the females for which three- and four-consecutive-year sequences, respectively, were recorded. Of 14 observations that deviated from this pattern, 12 involved doing neither and two involved both molting and spawning in one of the three or four consecutive summers.

PERCENTAGE MOLTING

Percentage molting among tagged lobsters declined with increasing size but was generally higher during 1984-86 than in 1976-78 (Table 8). Too few observations in 1984-86 precluded comparison for small (<81 mm CL) lobsters. Percentages among 81-90 mm animals were similar for males (chi-square test; P = 0.71) but significantly higher for females in 1984-86 (P < 0.05) and significantly higher for males (P = 0.03) and females (P< 0.01) in 1984-86 among larger (>90 mm) lobsters.

Within period size/sex comparisons showed differences that were not consistent between periods. During 1976-78, percentages molting were higher for males than females at 81-90 mm (P = 0.01) but similar for smaller and larger (P = 0.12) sizes. During 1984-86, however, they were similar for 81-90 mm lobsters of each sex (P = 0.63) but higher for females at the larger (>90 mm) sizes (P = 0.04).

DISCUSSION

Exploitation rates in lobster, *Homarus americanus*, fisheries tend to be quite high (Fogarty 1995); tagging studies therefore generally provide only single recaptures of individual lobsters of a limited size range (most tagged as pre-recruits) at liberty for relatively short periods. Closure of the Shag Rocks in Placentia Bay, Newfoundland to commercial fishing from 1976 to 1989 provided a unique opportunity for multiple recaptures over several years and the accumulation of observations of multi-consecutive-year life-history sequences, including molt increments, for individual lobsters.

Carapace length increment varied greatly among molts for individuals as it did also among lobsters. However, there was much inconsistency in the effect of various factors that were expected to contribute to the variability.

In fished populations around Newfoundland, molt increment normally increases with increasing premolt size in male lobsters while remaining the same in females (Ennis *et al.* 1982, 1986, 1989). This pattern was obtained from the 1984-1986 Shag Rocks data but for the data collected during 1976-78, when conditions would have been more comparable to a fished population, the slope of the premolt CL–molt increment relationship was zero for males and negative for females. There is no obvious explanation for the contrasting pattern at the Shag Rocks in 1976-78, but the change to a normal pattern in 1984-86 is linked to the shift to larger sizes while the population was closed to commercial fishing.

The molt cycle places heavy demands on physiological processes and, contrary to what might be expected (i.e. larger molt increments after longer intermolt periods), the statistical analysis indicates that molt increment is unaffected by the length of the intermolt period. The female reproductive cycle is also physiologically very demanding but appears not to limit energetic resources to an extent that somatic growth is affected. The analysis indicates that molt increment is unaffected by life-history events of the previous summer, even among females that molted and spawned or did neither.

The carapace length increment at a given molt evidently is inherently quite variable and it remains unclear what the main contributing factors might be.

Molting and spawning in alternate summers is clearly the norm among mature female lobsters. The increase from 79% of the females for which two-consecutive-year life-history sequences were recorded that followed this pattern in 1976-78 to 90% in 1984-86 is associated with the shift to larger sizes in the latter period. Most of the departures from this pattern involve molting and spawning in the same summer which is presumed to occur only in a portion of the animals spawning for the first time (Waddy *et al.*1995). Other departures were observed, however, and the drop to only 54% maintaining the alternate year sequence among those females (N=13) for which four-consecutive-year sequences were observed indicates that individual females do not maintain the normal, alternate year molt/spawn sequence consistently and indefinitely. Compared to males, the incidence of intermolt periods greater than 2 years was quite low among females. Physiological mechanisms involved in synchronizing the molt and reproductive cycles in females appear to reduce the

likelihood of long intermolt periods. This clearly is a factor in maintaining higher proportions molting annually among large females than among males of similar size.

Premolt-postmolt CL relationships and female life-history sequences are very important components of models used to assess the impact of changes in minimum legal size and exploitation rate in a lobster fishery on yield and egg production per recruit (Campbell 1985; Ennis 1985; Fogarty and Idoine 1988; Fogarty 1995). Estimation of postmolt CL is an especially important aspect of such modeling. The increase in weight at molting, the proportion that will molt or spawn during subsequent annual cycles of fishery and life-history events, the number of eggs produced by females that spawn, for example, depend heavily on the estimated postmolt CL. This study has shown that the slope of the premolt-postmolt CL relationship can be significantly different for data collected in the same area before and after substantive changes in the population. While the changes observed in the Shag Rocks population were due to closure to commercial fishing, changes in abundance or the level of exploitation, for example, might also alter the pattern of molt increment variation in relation to size. Despite being present in a lobster population in relatively small numbers, large lobsters will contribute quite substantially to output values from yield and egg per recruit models. The farther removed from current high values for exploitation rate and small size limits used in a modeling exercise, the greater the potential for unrealistic outputs associated with an unrepresentative premolt-postmolt CL relationship.

Biological relationships for lobster populations are usually based on a preponderance of observations on small animals because of high exploitation rates and small size limits that prevail in lobster fisheries. Results from this study show that due consideration must be given to potential biases associated with applying these relationships to larger lobsters in biological model populations.

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Table 1. Molt increments for male lobsters at the Shag Rocks,1976-78 and 1984-86.

Premolt CL (mm)	Molt Increments					
	1976-78			1984-86		
	N	Range	Mean	N	Range	Mean
61-70	2	16-20	18.0	-	-	-
71-80	32	7-20	14.2	2	9-11	10.0
81-90	76	5-24	12.6	24	8-14	11.8
91-100	41	6-23	13.6	17	6-16	11.9
101-110	10	6-21	14.0	26	5-17	13.5
111-120	3	9-11	10.0	14	10-20	14.5
121-130	-	-	-	3	9-17	14.3

Table 2. Molt increments for nonovigerous and ovigerous female lobsters at the Shag Rocks, 1976-78 and 1984-86.

Premolt CL (mm)	Molt Increments								
	1976-78						1984-86		
	Nonovigerous			Ovigerous			Ovigerous		
	N	Range	Mean	N	Range	Mean	N	Range	Mean
71-80	45	6-21	12.2	6	8-14	10.0	1	7	7.0
81-90	52	5-22	11.8	30	6-17	9.7	5	7-9	8.2
91-100	15	5-14	9.8	38	5-17	9.9	14	7-15	8.6
101-110	1	10	10.0	10	7-11	9.0	20	7-11	8.2

Table 3. Molt increments for all female lobsters at the Shag Rocks, 1976-78 and 1984-86.

Premolt CL (mm)	Molt Increments					
	1976-78			1984-86		
	N	Range	Mean	N	Range	Mean
61-70	1	14	14.0	-	-	-
71-80	51	6-21	11.9	3	7-11	9.0
81-90	82	5-22	11.0	12	7-10	8.3
91-100	53	5-17	9.8	25	5-15	8.5
101-110	11	7-11	9.1	24	5-11	8.1
111-120	-	-	-	18	6-16	8.4
121-130	-	-	-	5	6-11	7.8
131-140	-	-	-	1	9	9.0

Table 4. Variation in a second consecutive molt increment in relation to the first for male and female lobsters at the Shag Rocks.

		Variation in second molt increment compared to first			
		Range (mm)	Percent		
First molt premolt CL (mm)	N	Less than (-)/ Greater than (+)	Less	Same	Greater
Males					
71-80	5	-4 to +5	40	-	60
81-90	26	-7 to +6	19	8	73
91-100	18	-7 to +8	17	22	61
> 100	17	-2 to +2	67	-	33
Females					
71-80	12	-8 to +7	58	17	25
81-90	20	-5 to +4	35	10	55
91-100	18	-5 to +7	32	20	48
> 100	17	-9 to +2	35	30	35

Table. 5 Variation in a second consecutive molt increment for male and female lobsters at the Shag Rocks whose first increment was more than 1 standard deviation larger or smaller than the mean.

	First increment > 1 s.d. larger than the mean				First increment > 1 s.d. smaller than the mean			
		Second increment				Second increment		
First molt premolt CL (mm)	N	<	=	> first	N	<	=	> first
Males								
71-80	2	2	-	-	-	-	-	-
81-90	3	1	-	2	5	1	1	3
91-100	1	-	1	-	2	-	1	1
> 100	-	-	-	-	1	1	-	-
Females								
71-80	2	2	-	-	1	-	-	1
81-90	2	2	-	-	1	-	-	1
91-100	2	2	-	-	1	-	-	1
> 100	1	1	-	-	1	-	-	1

Table 6. Molt increments at 1- to 5- year intermolt periods for male and female lobsters at the Shag Rocks.

Premolt CL (mm)	1 Year			2 Years			3 Years			4 Years			5 Years		
	N	Range	Mean	N	Range	Mean	N	Range	Mean	N	Range	Mean	N	Range	Mean
Males	1	14	14.0				2	11-14	12.5						
81-90	3	11-15	13.7	4	11-14	13.3	6	8-16	11.3						
91-100	3	14-21	17.3	3	14-17	15.3	7	5-16	12.3						
101-110				1	18	18.0	6	11-17	14.0	1	20	20.0			
111-120							2	15-17	16.0				1	12	12.0
121-130															
131-140															
Females															
71-80				1	9	9.0									
81-90	3	6-17	11.3	25	6-22	9.6									
91-100	1	10	10.0	40	5-17	9.1									
101-110	2	6-10	8.0	19	6-11	8.6				2	5-6	5.5			
111-120				10	7-9	8.3									
121-130				6	6-11	8.2									
131-140				1	8	8.0									

Table 7. Percentage of various two-consecutive-year life-history sequences for female lobsters at the Shag Rocks, 1976-78 and 1984-86.

Premolt CL (mm)	N	Two-consecutive year sequences; One year-top, other year-bottom						
		Molt Molt	Molt Lay	Molt/Lay Molt	Molt/Lay Lay	Lay Lay	Molt Nothing	Lay Nothing
1976-78								
71-80	15	13.3	66.7	6.7	-	-	6.7	6.7
81-90	43	-	83.7	-	-	7.0	4.7	4.7
91-100	40	-	80.0	5.0	-	2.5	7.5	5.0
101-110	11	-	72.7	-	-	-	-	27.3
Totals	109	1.8	78.9	2.8	-	3.7	5.5	7.3
1984-86								
81-90	5	-	80.0	-	20.0	-	-	-
91-100	16	-	93.8	-	6.3	-	-	-
101-110	23	-	95.7	-	-	4.3	-	-
111-120	15	-	93.3	-	-	6.7	-	-
121-130	3	-	33.3	-	-	-	-	66.7
Totals	62	-	90.3	-	3.2	3.2	-	3.2

Table 8. Percentage molting in a given summer among sphyrion-tagged lobsters at the Shag Rocks, 1976-78 and 1984-86.

	1976-78		1984-86	
Premolt CL (mm)	N	% molting	N	% molting
Males				
71-80	37	86.5	3	66.7
81-90	134	56.7	40	60.0
91-100	147	27.9	47	36.2
101-110	82	12.2	77	33.8
111-120	25	12.0	47	29.8
121-130	5	0.0	30	10.0
Females				
71-80	62	82.3	4	75.0
81-90	193	42.5	18	66.7
91-100	172	30.8	59	42.4
101-110	57	19.3	59	40.7
111-120	6	0.0	49	36.7
121-130	-	-	23	21.7

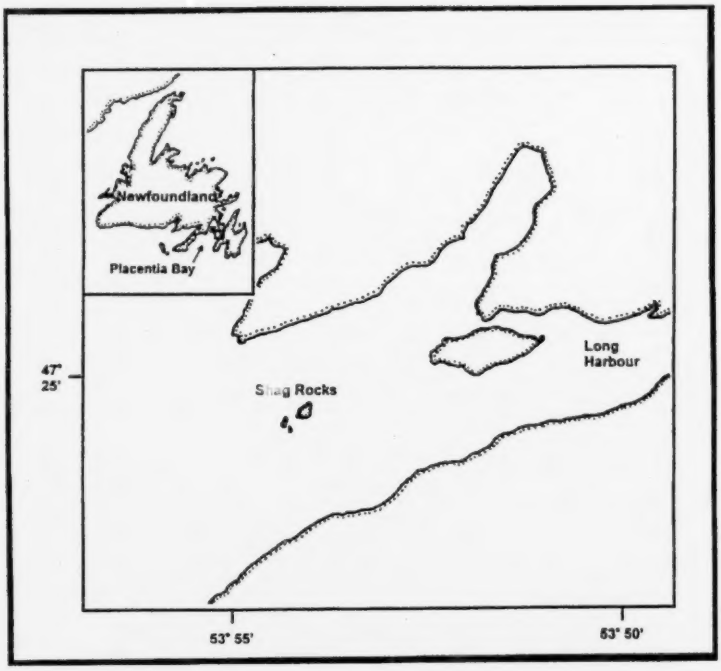

Fig. 1. Map of Newfoundland and the Shag Rocks (location indicated in insert), the area in Placentia Bay closed to commercial lobster fishing from 1976 to 1989.

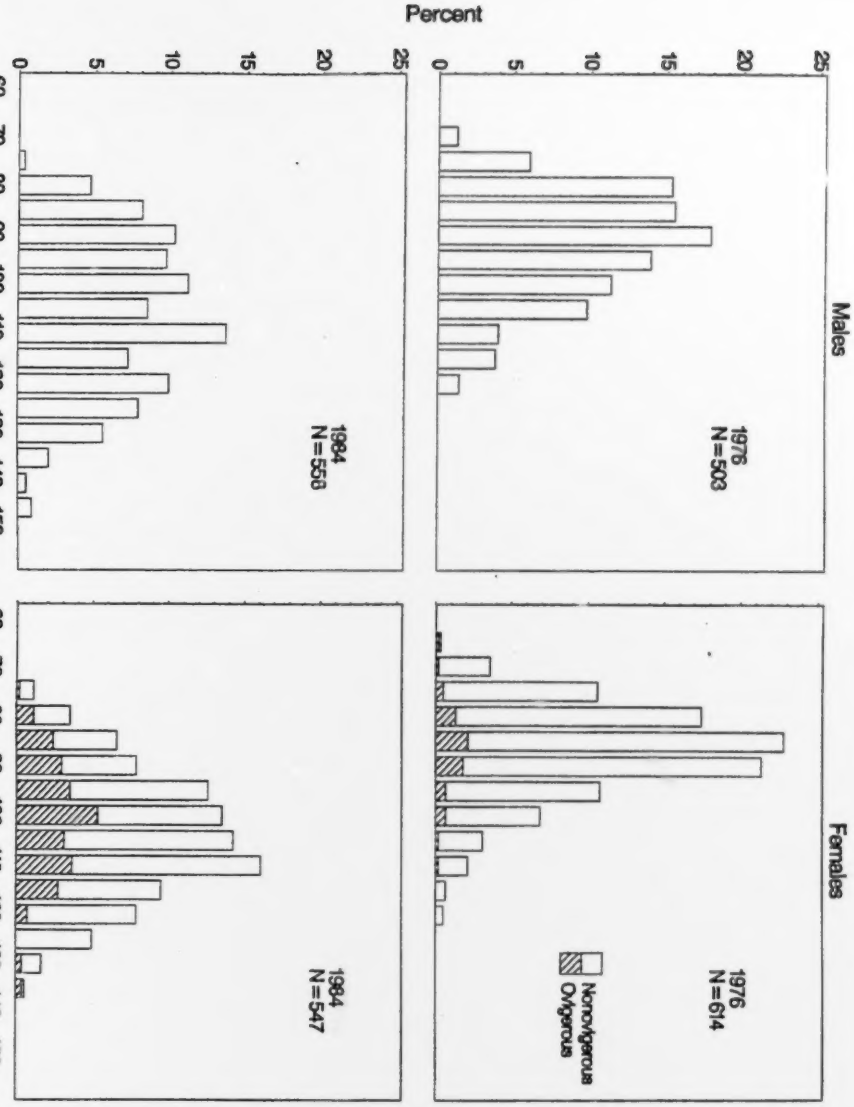

Fig. 2. Composition of lobsters caught at the Shag Rocks during May–June research trap fishing in 1976 and 1984.

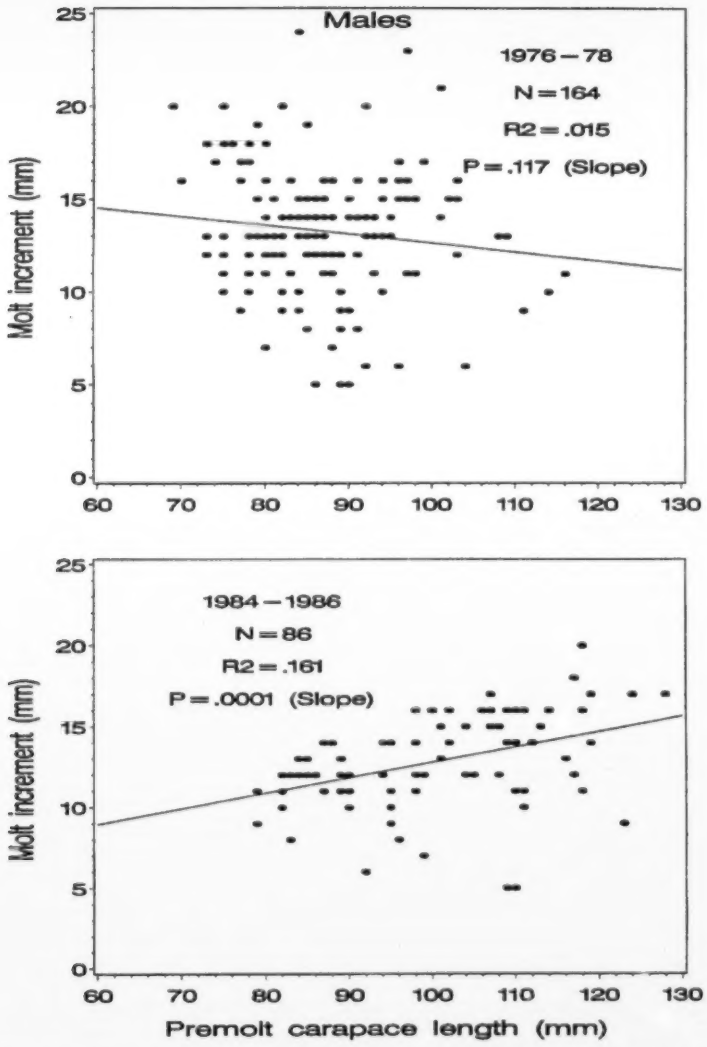

Fig. 3. Premolt CL–molt increment regressions for male lobsters at Shag Rocks, 1976–78 and 1984–86.

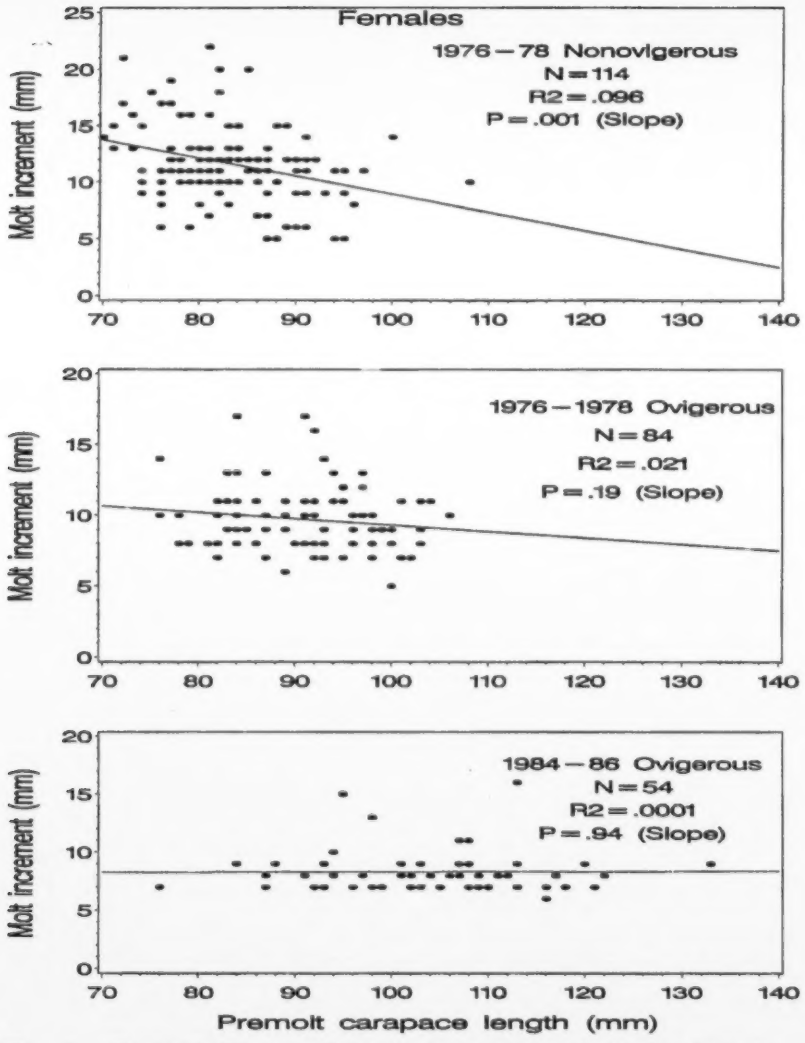

Fig. 4. Premolt CL—molt increment regressions for female lobsters at Shag Rocks, 1976—78 and 1984—86.

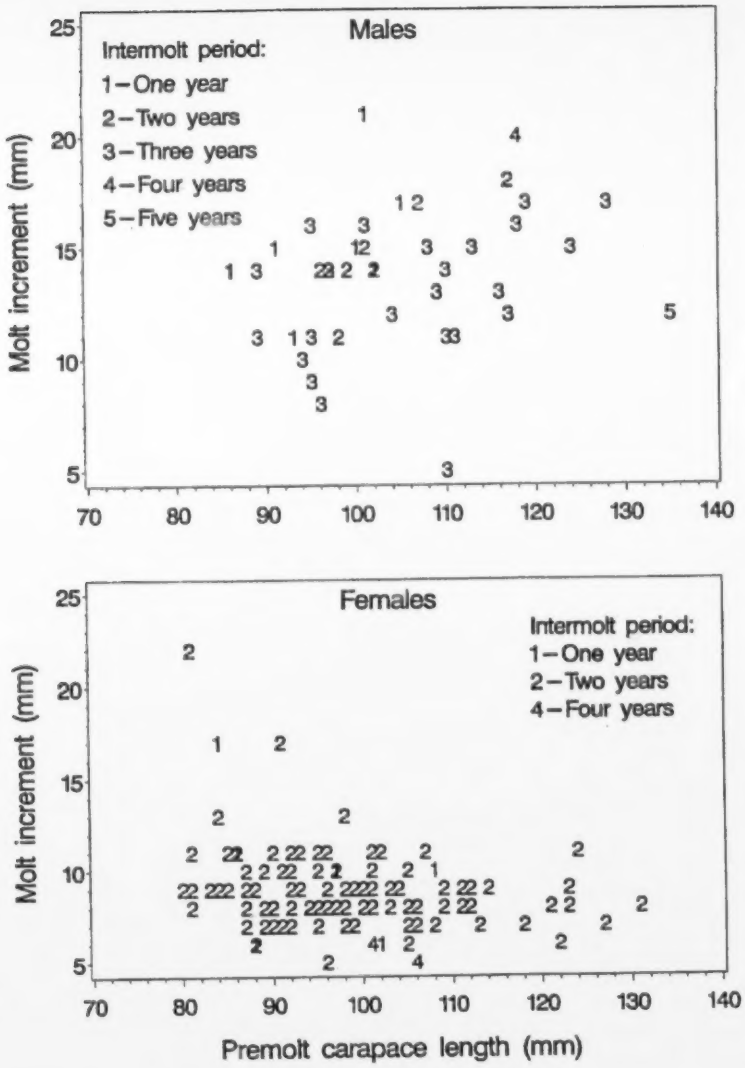

Fig. 5. Plots of molt increment in relation to premolt CL at 1 to 5 year intermolt periods for male and female lobsters at the Shag Rocks.

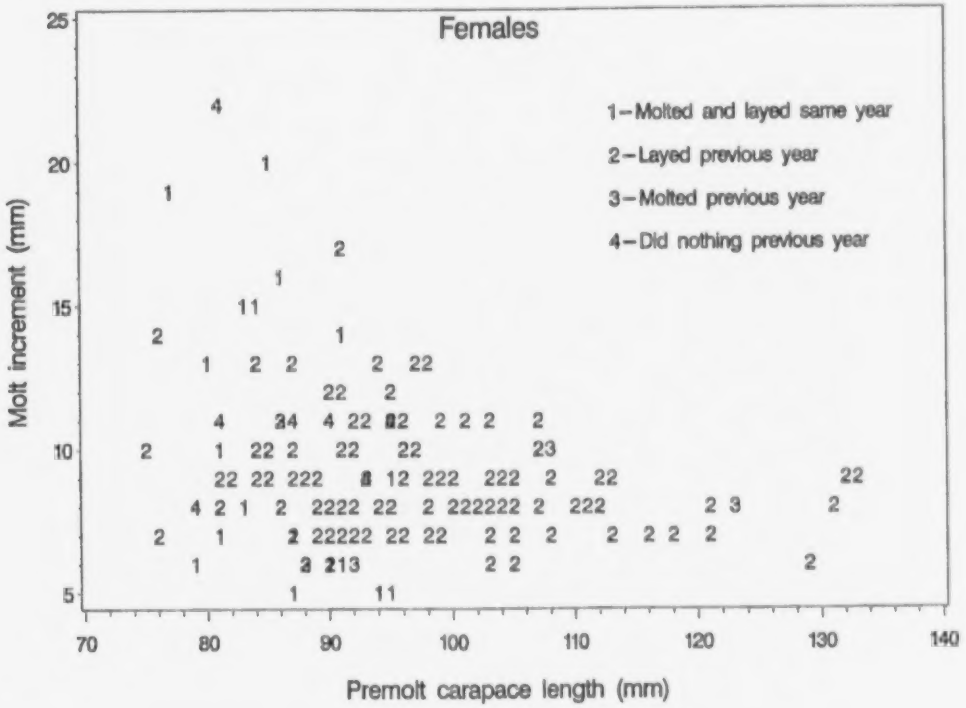

Fig. 6. Plots of molt increment in relation to premolt CL following various life–history events for female lobsters at the Shag Rocks.

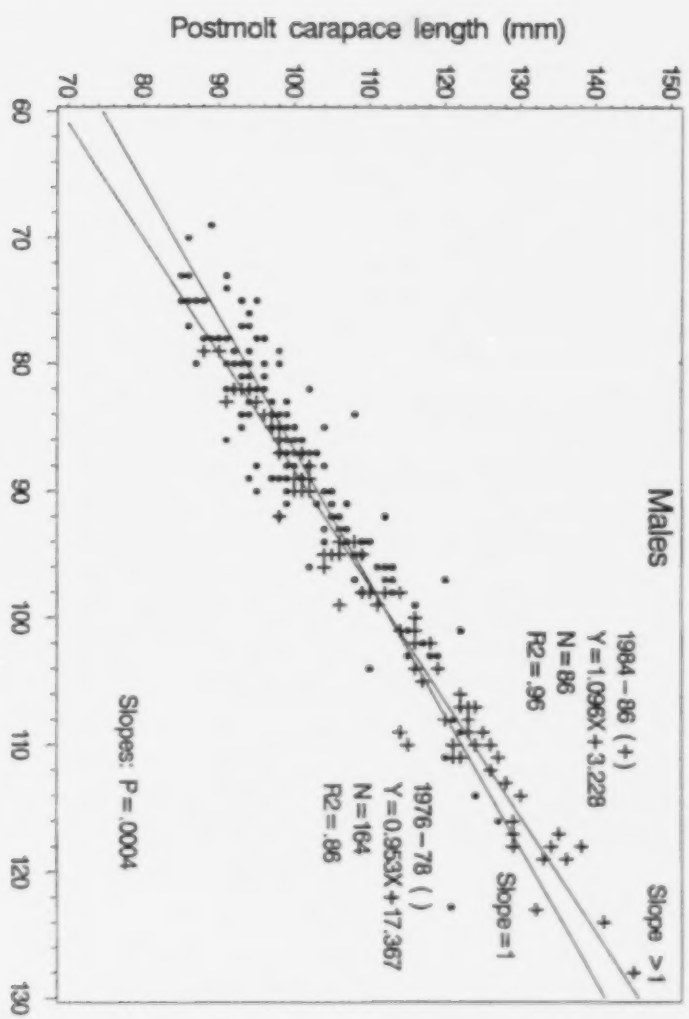

Fig. 7. Premolt–postmolt CL relationships for male lobsters at the Shag Rocks, 1976–78 and 1984–86 .

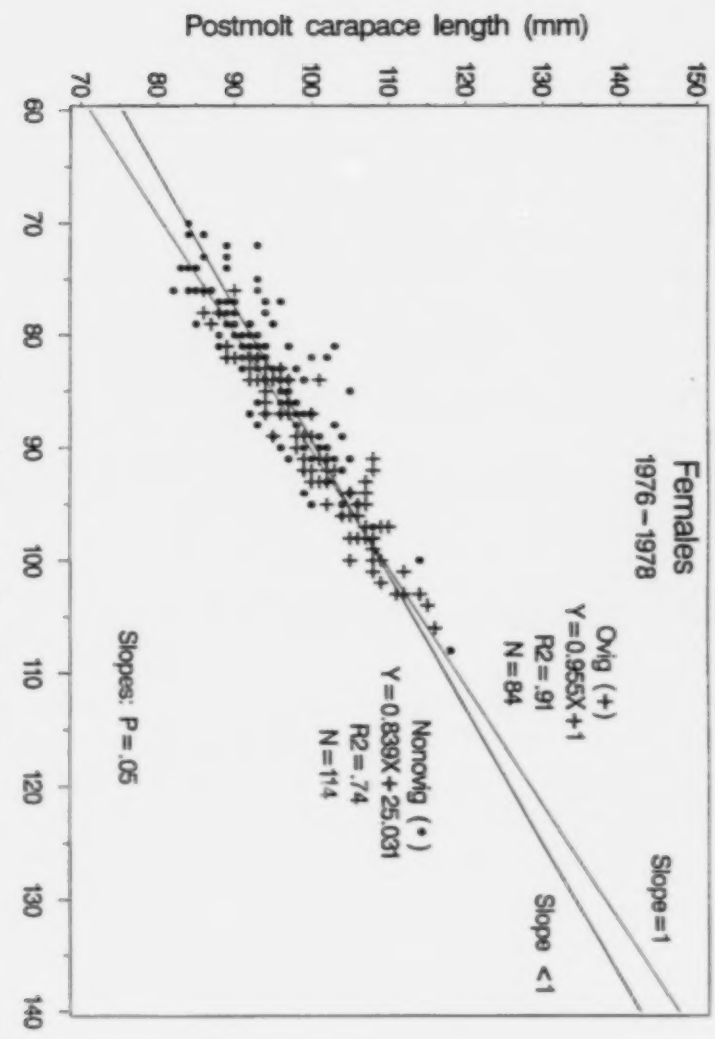

Fig. 8. Premolt–postmolt CL relationships for ovigerous and nonovigerous females at the Shag Rocks in 1976–78.

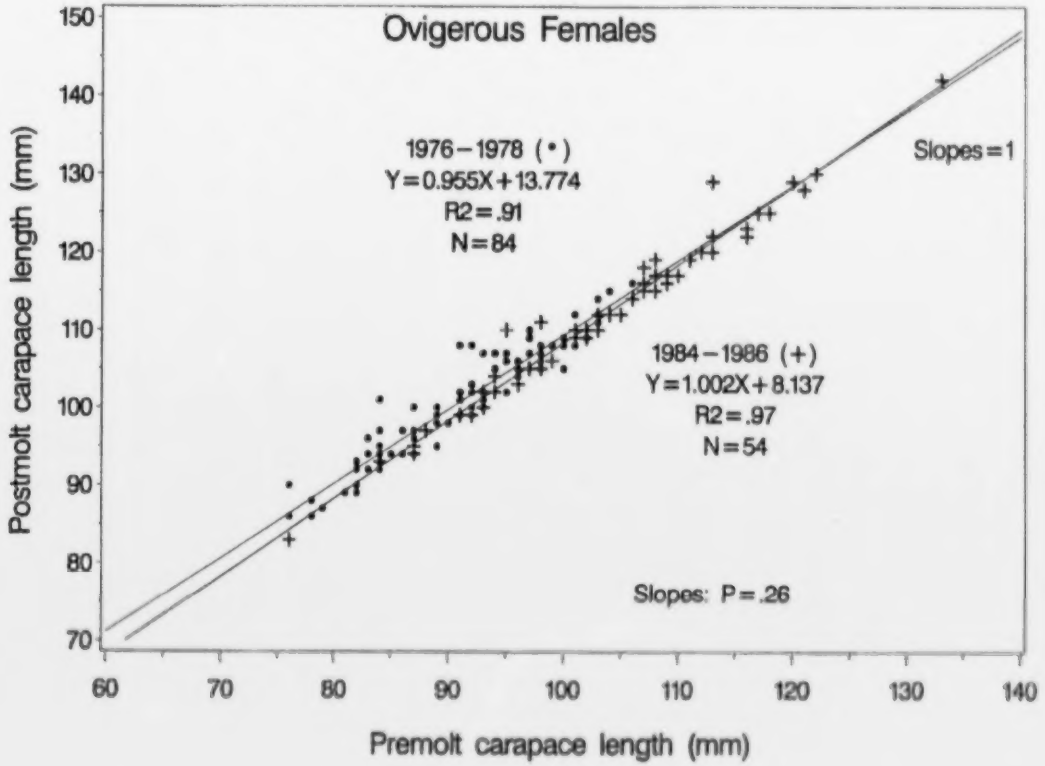

Fig. 9. Premolt–postmolt CL relationships for ovigerous female lobsters Shag Rocks, 1976–78 and 1984–86.

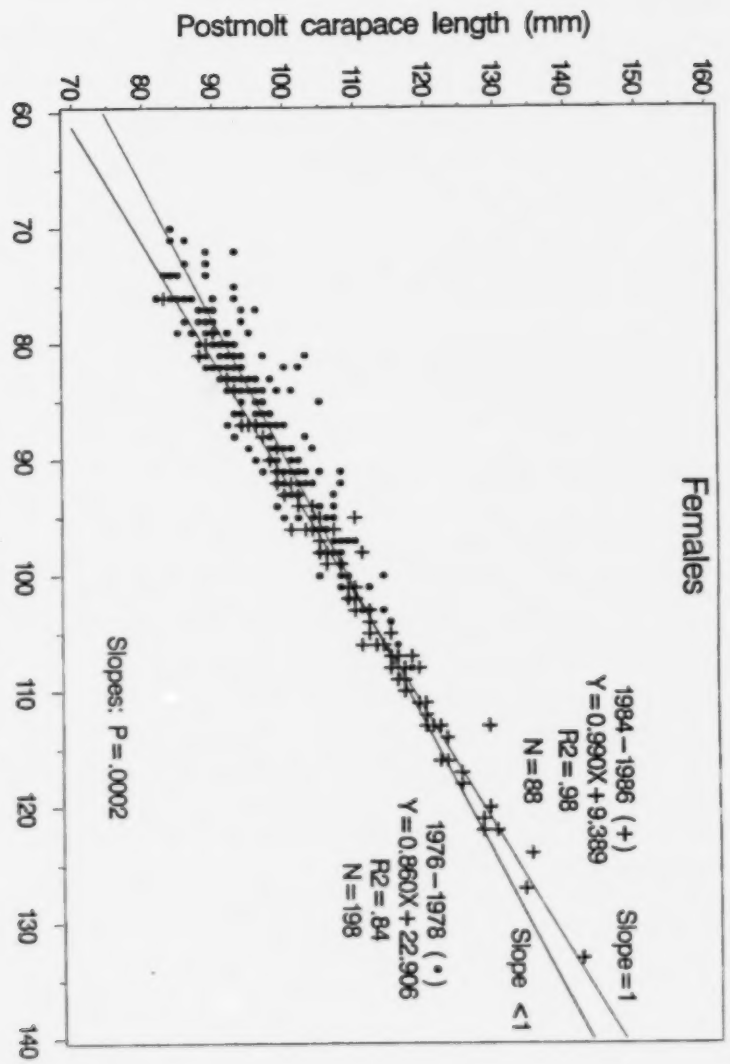

Fig. 10. Premolt–postmolt CL relationships for all female lobsters at the Shag Rocks, 1976–78 and 1984–86.